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# Cohort-splitting in the millipede *Polydesmus angustus* (Diplopoda: Polydesmidae): No evidence for maternal effects on life-cycle duration

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**Key words.** Diplopoda, *Polydesmus angustus*, life cycle, development time, diapause, maternal effect, bet-hedging

**Abstract.** Under seasonal conditions, *Polydesmus angustus* individuals born in the first part of the breeding season have a 1-year life cycle and those born later have a 2-year life cycle (cohort-splitting). In this study, 249 juveniles from four early broods (born in mid-July) and four late broods (born in September) were reared under similar laboratory conditions, to test for possible maternal influences on life-cycle duration. Development times of early- and late-born individuals were compared under four combinations of day length and temperature (16 h – 18°C, 16 h – 16°C, 12 h – 18°C and 12 h – 16°C). The results showed that development time varied significantly in response to day length, temperature and sex, but that of individuals in the early and late broods did not differ significantly (mean development times ± SE: 180 ± 6 and 183 ± 8 days, respectively). There were no significant interactions between birth period and other factors, indicating that the effects of day length, temperature and sex on development time were similar in early- and late-born individuals. This indicates that the extended life cycle of millipedes born late in the season is not maternally determined and that cohort-splitting is controlled entirely by the environmental conditions experienced by the offspring during their development. This conclusion is supported by the absence of significant variation in offspring live weight at birth measured at different times in the breeding season. The results are discussed in relation to the bet-hedging theory, which is often put forward to account for cohort-splitting in arthropods. In *P. angustus*, the results are consistent with either bet-hedging or adaptive plasticity, but further studies are required to decide which interpretation is correct.

## INTRODUCTION

In many arthropods with relatively long life cycles (≥ 1 year), the cohort of individuals born in the same breeding season splits into groups that reproduce in different years. This phenomenon of cohort-splitting (Sunderland et al., 1976), also called parsivoltinism in insects (Torchio & Tepedino, 1982), is reported in woodlice (Sunderland et al., 1976; Zimmer & Kautz, 1997), millipedes (Snider, 1984; David et al., 1993), spiders (Bonte & Maelfait, 2001) and insects, aquatic and terrestrial (e.g. Pritchard, 1980; Moreira & Peckarsky, 1994; Danforth, 1999; Menu & Desouhant, 2002). In some species, the split is sex-specific (Gonçalves et al., 2005).

Cohort-splitting can result from a variety of biological mechanisms, such as: (1) distinct recruitment periods coupled with environmental conditions experienced during development, as in the woodlouse *Philoscia muscorum* (Scopoli) (Grundy & Sutton, 1989); (2) a genetic polymorphism, as in the butterfly *Maculinea rebeli* (Hirschke) (Thomas et al., 1998); and (3) maternal effects, which can control offspring development not only at the egg stage but also later in the life cycle (Mousseau & Dingle, 1991). Clarifying the mechanism involved is important because cohort-splitting is often interpreted as diversified bet-hedging, i.e. phenotypic variation that spreads the risks of a population crash in unpredictable environments, which is incompatible with genetic polymorphism (Seger & Brockmann, 1987; Stearns, 1992; Hopper, 1999). In addition, bet-hedging is more likely to occur when maternal effects control life-cycle duration a long time in advance, whereas plasticity based on environmental cues during offspring development is more likely to be an adaptation to predictable conditions (Hopper, 1999; Roff, 2002).

In the temperate millipede *Polydesmus angustus* Latzel, an individual's life cycle depends on its month of birth (David et al., 1999; David, 2009). That of individuals born early in the breeding season (May – August) is annual, and those born later (August – early October) biennial, irrespective of the parental life cycles (David, 2009). Biennial individuals undergo two periods of diapause: (1) they aestivate in the penultimate stadium (stadium VII) during the first breeding season after their birth, and reach maturity in early autumn; (2) adult females that emerge in autumn do not reproduce immediately; they overwinter a second time and reproduce in the second breeding season after birth (David et al., 1999). Aestivation and reproductive diapause are, at least in part, under photoperiodic control (David et al., 2003a): exposure to long days at stadia VI–VII promotes aestivation and increases the duration of development in most individuals, whereas short days (≤ 12 h) lengthen the preoviposition period in all adult females. In a seasonal environment, late-born individuals reach stadia VI–VII in spring, experience long-day conditions and are channelled towards a biennial cycle by a two-stage photoperi-

odic response, as in certain insects (Tauber et al., 1986; Butterfield et al., 2001).

Environmental control of development, however, does not rule out constitutive differences between individuals (Danks, 1987, 2002). In *P. angustus*, the occurrence of photoperiodically induced diapause only in late-born offspring suggests that they might be predisposed for longer life cycles. There is no possibility of genetic polymorphism for life-cycle duration in this millipede, because biennial offspring are produced almost exclusively by annual females (David, 2009). However, a non-genetic maternal effect might extend the development of individuals born late in the season. In many insect species, mothers that experience decreasing photoperiods and temperatures produce offspring that show an increased incidence of diapause (Mousseau & Dingle, 1991; Fox & Mousseau, 1998). Maternal age also affects the development of offspring and their tendency to enter diapause (Danks, 1987; Mousseau & Dingle, 1991). In a number of species, changes in egg size mediate this maternal age effect: older females lay smaller eggs, which develop more slowly (Mousseau & Dingle, 1991; Fox & Czesak, 2000).

The main objective of this study was to determine whether development time is longer in millipedes born in late summer than in those born earlier when all are reared under identical conditions. This would indicate inherited differences between the two groups, i.e. non-genetic maternal effects in the case of *P. angustus*. This issue cannot be tested in a seasonal environment, where the two groups would not develop under the same photoperiod and temperature conditions, but requires controlled laboratory conditions. It must, however, be tested in a variety of environments, because the expression of the maternal effect may depend not only on the maternal environment, but also on that of the offspring (Rossiter, 1998). Moreover, comparisons between early- and late-born individuals under a set of environmental conditions make it possible to test whether they respond in the same way to abiotic factors, especially photoperiod, which is a key factor in the induction of aestivation.

The second objective was to determine whether the live weight of newly hatched offspring decreases in the course of the breeding season and/or in relation to the age of the females. In insects, development rate generally shows a positive relationship with egg size or weight (Rossiter, 1991; Azevedo et al., 1997; Mohaghegh et al., 1998), and any decrease in offspring size at birth could be indicative of a maternal effect that affects future offspring development.

## MATERIAL AND METHODS

### Biological material

The temperate millipede *P. angustus* is widespread in north-western Europe, mainly in woodland, where it feeds on decaying plant material. This species has a long period of reproduction in spring-summer, during which each female produces several broods at intervals of a few weeks before dying (David, 2009). Eggs are laid in nests made of earthy faecal material, and first stadium juveniles leave the nest soon after hatching. The post-embryonic development consists of eight stadia (= instars), which can be identified by counting the number of body rings, and the sexes can be distinguished from stadium IV onwards (Enghoff et al., 1993). In a seasonal environment, development time from egg hatch to adult emergence lasts about 10 months for annual individuals, plus a further 3 months in aestivation for biennial individuals (David et al., 1999).

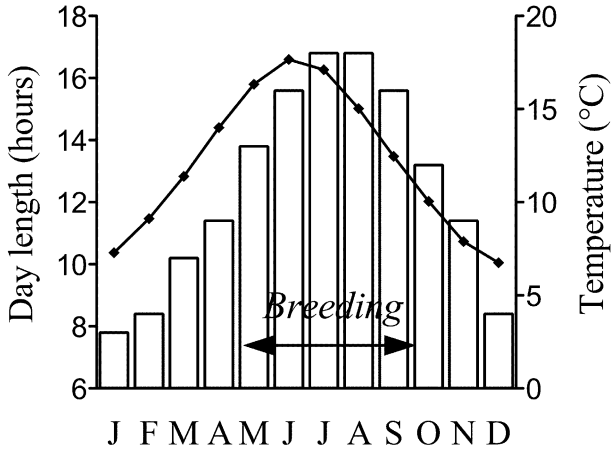


Fig. 1. Standard seasonal conditions in which *Polydesmus angustus* adults were reared to produce the juveniles used in the experiments. Line: naturally varying day length. Bars: controlled temperatures. The double ended arrow above the x-axis indicates the breeding period.

This study was conducted on *P. angustus* specimens from Brunoy, 20 km south-east of Paris. They were born to adults either collected from the field in early spring or reared in the laboratory under standard seasonal conditions (Fig. 1). The adults were kept in male-female pairs in transparent plastic boxes (400 ml) containing about 1 cm of sieved soil and moist leaf litter. The boxes were placed in LMS incubators fitted with a glass door and exposed to the natural photoperiod of Montpellier, southern France, which results in life cycles similar to those recorded at the Brunoy photoperiod (David et al., 1999). Temperature followed the mean monthly temperatures of the region of origin, with a daily thermoperiod of 4°C (Fig. 1).

### Development time of early- and late-born millipedes reared under similar conditions

Following the reproduction of the females kept in the standard seasonal environment, first stadium juveniles born early (mid-July) and late (September) in the breeding season were reared to maturity under identical temperature and photoperiod conditions. All were transferred within 4 days of hatching to one of four LMS incubators fitted with a steel door and controlled lighting. Two incubators were set at 16°C (thermophase of 18°C for 12 h and cryophase of 14°C for 12 h) under long (16L : 8D) and short (12L : 12D) photoperiods, and two were set at 18°C (thermophase of 20°C for 12 h and cryophase of 16°C for 12 h) under long (16L : 8D) and short (12L : 12D) photoperiods. Juveniles from four early broods and four late broods were evenly distributed among the four incubators, with about 20–30 millipedes from each brood in each incubator. They were kept in the same culture boxes as those mentioned above. They were fed ad libitum on a mixture of hornbeam, chestnut, hazel and oak leaf litter previously rinsed in distilled water, and were given a pinch of dry yeast (*Saccharomyces cerevisiae* Hansen) every month to standardize food conditions. Survivors were sexed from stadium IV onwards and small random samples from each brood (about 4 males and 4 females) were distributed into

TABLE 1. Results of the ANOVA of the effects of birth period (early vs. late), day length (12 h vs. 16 h), temperature (16°C vs. 18°C) and sex on the development time of *Polydesmus angustus*. Figures in bold indicate significant effects and interactions at the 5% level.

| Source of variation | $F_{1,6}$ | Probability | Means ± SE (days) |
|---|---|---|---|
| Birth period (P) | 0.06 | 0.82 | early: 180 ± 6 / late: 183 ± 8 |
| Day length (L) | **48.98** | **0.0004** | 12 h: 156 ± 3 / 16 h: 207 ± 7 |
| P × L | 1.77 | 0.23 | |
| Temperature (T) | **14.74** | **0.009** | 16°C: 174 ± 6 / 18°C: 189 ± 8 |
| P × T | 0.59 | 0.47 | |
| Sex (S) | **16.17** | **0.007** | males: 170 ± 5 / females: 193 ± 8 |
| P × S | 0.02 | 0.90 | |
| L × T | **20.9** | **0.004** | 12 h – 16°C: 159 ± 4 / 12 h – 18°C: 152 ± 4<br>16 h – 16°C: 189 ± 9 / 16 h – 18°C: 226 ± 8 |
| P × L × T | 1.06 | 0.34 | |
| L × S | **8.21** | **0.03** | 12 h – males: 151 ± 3 / 12 h – females: 161 ± 4<br>16 h – males: 189 ± 8 / 16 h – females: 226 ± 10 |
| P × L × S | 0.01 | 0.91 | |
| T × S | 0.01 | 0.93 | |
| P × T × S | 0.41 | 0.55 | |
| L × T × S | 1.05 | 0.35 | |
| P × L × T × S | 0.03 | 0.86 | (see Fig. 2) |

several boxes to reduce population density. Development time from egg hatch to adult emergence was assessed by examining the boxes twice a week, i.e. with an error ≤ 4 days. The experiment yielded results for a total of 249 individuals (124 females and 125 males), i.e. a mean of 7.8 individuals from each brood in each incubator.

**Offspring live weight at birth**

The live weight of offspring born under seasonal conditions in the laboratory was determined. As eggs of *P. angustus* are difficult to weigh exactly, due to extremely high rates of water loss (David et al., 2003b), first stadium juveniles were weighed instead. Within 4 days of hatching, batches of about 20 juveniles were collected from dead leaves in each culture box and rapidly transferred with a brush into a small dish. The dish was promptly examined under a stereomicroscope to remove any impurities and then weighed on a Sartorius balance (sensitivity 0.1 mg). The juveniles were removed with a brush, counted, and the empty dish was re-weighed. The mean offspring live weight was obtained by dividing the total weight by the number of individuals. Juveniles with an empty gut, i.e. within a few hours of hatching, were not taken into account to eliminate this cause of variation.

To test for changes in offspring live weight in the course of the breeding season, juveniles born during the first month of reproduction (10 May–10 June), in the middle of the season (7–26 July) and at the end of the season (28 August–7 October) were compared. The data came from 25 broods produced by 18 different females in different years.

To test for changes in offspring live weight during the reproductive life of individual females, only females that completed their development in the laboratory were used, so that the exact number of broods they produced was known. For eight females that produced a relatively large number of broods, the live weights of juveniles from broods 1, 3 and 5 were compared.

**Statistical analyses**

In the experiment performed under constant environmental conditions, the effects of birth period (early vs. late), day length (12 h vs. 16 h), temperature (16°C vs. 18°C) and sex on the development time of millipedes were tested using multiway ANOVA. In a partly hierarchical design, the broods (4 early and 4 late) were nested within periods, while day length, temperature and sex were fixed factors crossed across broods and periods. In this model, the appropriate error term for the period effect was the brood effect within periods, and all effects involving crossed factors were tested over their interaction with the brood effect within periods (Quinn & Keough, 2002). The data were the means for each combination of factors, i.e. without replication, as in the classical split-plot design (Quinn & Keough, 2002).

Changes in offspring live weight during the breeding season were tested using one-way ANOVA and those measured during the reproductive life of females were tested using two-way ANOVA without replication (simple repeated measures design).

## RESULTS

### Development time of early- and late-born millipedes reared under similar conditions

When individuals from the same broods were reared in the four photoperiod-temperature combinations, the results of the ANOVA showed that development time did not differ significantly between early and late broods (Table 1). Mean development times, averaged across all conditions, were 180 ± 6 and 183 ± 8 days for early- and late-born individuals, respectively. There was a highly significant effect of day length, with development times markedly longer at 16 h than at 12 h ($P < 0.001$). This was due to longer times spent in the last two immature stadia, especially stadium VII, under long-day conditions. There was however a strong interaction between temperature and day length ($P < 0.01$). Examination of the means revealed that the effect of long days on development time was markedly stronger at 18°C (+ 74 days) than at 16°C (+ 29 days). As a result, development time was a little shorter at 18°C than at 16°C under short-day conditions, but much longer at 18°C than at 16°C under long-day conditions (Table 1). There was also a significant effect of sex, with longer development times in females than in males ($P < 0.01$). The absence of any significant interaction between those factors and birth periods indicates that

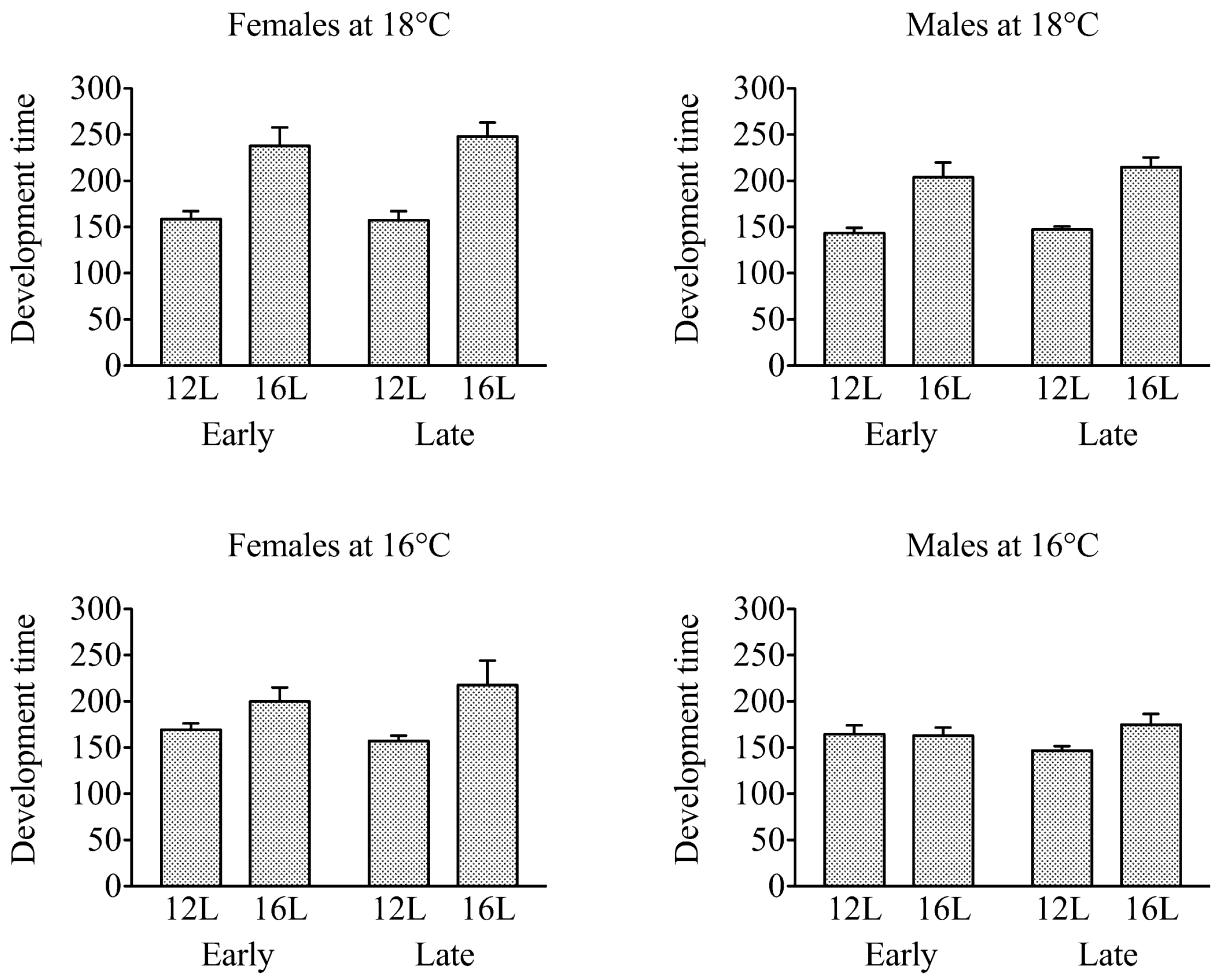


Fig. 2. Development times (from egg hatch to adult emergence, in days) of *Polydesmus angustus* millipedes born early and late in the season and reared under similar conditions in the laboratory. Results are shown for each sex at two temperatures (18 and 16°C) and two day lengths (12 and 16 h).

the effects of day length, temperature and sex were similar in millipedes from early and late broods.

Detailed results for each birth period, day length, temperature and sex are summarized in Fig. 2. At 18°C, there were very small differences in development time between early and late broods, whatever the sex or the day length. Slightly larger differences between early and late broods occurred at 16°C, especially in males, but they were not large enough to be significant.

**Offspring live weight at birth**

Under seasonal conditions, no significant differences in live weight were observed between first stadium individuals born in the first month of reproduction (54.1 ± 1.8 µg; n = 9 broods), in the middle of the breeding season (56.7 ± 3.1 µg; n = 8) and at the end of the breeding season (57.7 ± 2.3 µg; n = 8) (one-way ANOVA: $F_{2,22}$ = 0.63; P = 0.54).

No significant variation in offspring live weight was observed during the reproductive life of individual females. In eight females that produced at least five broods, two-way ANOVA showed that the live weight of first stadium individuals did not vary significantly among broods 1, 3 and 5 ($F_{2,14}$ = 0.69; P = 0.52). On average, the smallest offspring were those from the first brood (53.6 ± 1.3 µg) and the largest, those from the fifth brood (56.6 ± 2.2 µg).

**DISCUSSION**

Cohort-splitting, i.e. the occurrence of different types of life cycles among individuals born in the same breeding season (Sunderland et al., 1976) is widespread in arthropods. In most cases, however, the mechanisms involved are unknown and the significance of this phenomenon is unclear. The prevailing interpretation is bet-hedging (Danks, 2007), i.e. risk-spreading in unpredictable environments, which has rarely been tested rigorously (Hopper, 1999).

In the temperate millipede *P. angustus*, the duration of the life cycle under mean seasonal conditions increases from 1 year for individuals born early in the season to 2 years for those born later (David et al., 1999). The extended life cycle results from a delay in development, due to aestivation in stadium VII, combined with the adult females overwintering in reproductive diapause. In a previous study, it was shown that biennial offspring are produced almost exclusively by annual females, so this pattern cannot be determined genetically (David, 2009).

In the present study the hypothesis that the propensity of late-born individuals to aestivate results, at least in part, from a non-genetic maternal effect, was tested. The results of rearing early- and late-born offspring under similar environmental conditions did not support this hypothesis. Across four combinations of day length and temperature, mean development times were virtually the same for both groups, differing by less than 2% on average. Moreover, the absence of interactions between birth period and abiotic factors indicates that the effects of day length and temperature on development time were similar in early- and late-born individuals. For example, long days at 18°C markedly increased development time, which mimics what occurs during aestivation, with similar increases recorded for early- and late-born individuals. Subject to confirmation by rearing individuals over a greater range of environmental conditions, it can be concluded that no maternal effects influence the development of offspring born towards the end of the season.

This conclusion is reinforced by the absence of significant changes in the live weight of newly hatched offspring, whether during the breeding season or the reproductive life of females. Maternal effects on insect development are often mediated by changes in egg size or weight (Mousseau & Dingle, 1991; Fox & Czesak, 2000), probably due to positive correlations between egg size and egg quality (Giron & Casas, 2003). Typically, older females lay smaller eggs, which develop more slowly, as in the seed beetles *Callosobruchus* spp. Fabricius (Fox, 1993; Yanagi & Miyatake, 2002). This mechanism does not appear to be involved in the extended life cycle of late-born *P. angustus*.

All the evidence suggests that in this millipede, cohort-splitting results only from environmentally-controlled adjustments during development. First, the developmental switch in spring, which leads to either rapid maturation (1-year life cycle) or aestivation in stadium VII, is controlled by photoperiod (David et al., 2003a). The results of this study confirm that long days delay maturity, and further show that this effect is significantly reinforced by high temperatures. Following aestivation, females maturing in autumn enter diapause for several months in response to decreasing day lengths and temperatures, which results in the 2-year life cycle (David et al., 2003a). Cohort-splitting in the millipede *P. angustus* resembles what happens in the woodlouse *P. muscorum*, another saprophagous macroarthropod living in similar habitats. In both species, early- and late-born individuals reared under similar conditions develop at similar rates, but their life cycles differ in a seasonal environment (Grundy & Sutton, 1989). However, temperature is the main factor regulating the life cycle of *P. muscorum*, whereas photoperiod is more important in *P. angustus*. In this millipede, there is a two-stage photoperiodic response, which is similar to that observed in a phytophagous insect, the heather psyllid *Strophingia ericae* (Curtis) (Butterfield et al., 2001).

From an evolutionary perspective, the question is why these species have evolved responses to environmental cues that channel a proportion of immatures towards a 2-year life cycle. Cohort-splitting is often regarded as diversified bet-hedging, which spreads the risks of a population crash in unpredictable environments (Danforth, 1999; Masaki, 2002; Menu & Desouhant, 2002; Kiss & Samu, 2005; Danks, 2007). Bet-hedging implies purely phenotypic variation that decreases temporal variation in fitness, at the cost of a lower arithmetic mean fitness (Seger & Brockmann, 1987; Stearns, 1992; Hopper, 1999). However, these conditions are rarely examined in empirical studies (Hopper, 1999). Even when variation in life-cycle duration is clearly not genetically determined, as in *P. angustus*, this is not evidence for bet-hedging. An alternative hypothesis is adaptive developmental plasticity, which increases individual fitness (Nylin & Gotthard, 1998). As a rule, adaptive plasticity is suspected when different phenotypes are produced in response to environmental cues during development (Hopper, 1999; Roff, 2002). In the woodlouse *P. muscorum*, cohort-splitting is interpreted in this way by Grundy & Sutton (1989), who concluded that, as the end of summer approaches, it is beneficial for females to trade off immediate breeding against further growth, with an increased reproductive potential the next year.

In *P. angustus*, cohort-splitting can be interpreted in two ways. (1) In terms of the bet-hedging hypothesis: long days in spring may herald the approach of summer and therefore the possibility of drought, a very unpredictable event in temperate areas, and cohort-splitting may be an insurance against a catastrophic loss of recruits. It is worth noting that juveniles are highly susceptible to desiccation, unlike individuals that aestivate in stadium VII, which are much more resistant (David & Vannier, 2001; David et al., 2003b). However, this is bet-hedging only if entering aestivation at stadium VII results in a fitness cost, i.e. if there is no individual compensation for the longer generation time. (2) Alternatively, day length in spring could be used as a cue to predict the time available to reach maturity and reproduce before the end of the first breeding opportunity, i.e. before the adult females enter diapause in early autumn. When there is insufficient time, individuals are channelled towards a 2-year life cycle and skip the first breeding season. This may be adaptive, if diapausing adult females have a better chance of surviving the winter than juveniles overwintering in early stadia, and if females reproducing in the second breeding season have a greater fecundity, as in *P. muscorum* (Grundy & Sutton, 1989). It is no longer bet-hedging if entering aestivation at stadium VII results in increased individual fitness. Further studies are required to decide which of these interpretations is correct in *P. angustus*.

## REFERENCES


Azevedo R.B.R., French V. & Partridge L. 1997: Life-history consequences of egg size in Drosophila melanogaster. *Am. Nat.* **150**: 250–282.

Bonte D. & Maelfait J.P. 2001: Life history, habitat use and dispersal of a dune wolf spider (Pardosa monticola (Clerck, 1757) Lycosidae, Araneae) in the Flemish coastal dunes (Belgium). *Belg. J. Zool.* **131**: 145–157.

BUTTERFIELD J., WHITTAKER J.B. & FIELDING C.A. 2001: Control of the flexible annual/biennial life cycle of the heather psyllid Strophingia ericae. *Physiol. Entomol.* **26**: 266–274.

DANFORTH B.N. 1999: Emergence dynamics and bet hedging in a desert bee, Perdita portalis. *Proc. R. Soc. Lond. (B)* **266**: 1985–1994.

DANKS H.V. 1987: *Insect Dormancy: An Ecological Perspective.* Biological Survey of Canada (Terrestrial Arthropods), Ottawa, 439 pp.

DANKS H.V. 2002: The range of insect dormancy responses. *Eur. J. Entomol.* **99**: 127–142.

DANKS H.V. 2007: The elements of seasonal adaptations in insects. *Can. Entomol.* **139**: 1–44.

DAVID J.F. 2009: Female reproductive patterns in the millipede Polydesmus angustus (Diplopoda: Polydesmidae) and their significance for cohort-splitting. *Eur. J. Entomol.* **106**: 211–216.

DAVID J.F. & VANNIER G. 2001: Changes in desiccation resistance during development in the millipede Polydesmus angustus. *Physiol. Entomol.* **26**: 135–141.

DAVID J.F., CELERIER M.L. & GEOFFROY J.J. 1999: Periods of dormancy and cohort-splitting in the millipede Polydesmus angustus (Diplopoda: Polydesmidae). *Eur. J. Entomol.* **96**: 111–116.

DAVID J.F., COURET T. & CELERIER M.L. 1993: The life cycle of the millipede Polydesmus angustus: another case of cohort-splitting. *Eur. J. Soil Biol.* **29**: 117–125.

DAVID J.F., GEOFFROY J.J. & CELERIER M.L. 2003a: First evidence for photoperiodic regulation of the life cycle in a millipede species, Polydesmus angustus (Diplopoda: Polydesmidae). *J. Zool. (Lond.)* **260**: 111–116.

DAVID J.F., GEOFFROY J.J. & VANNIER G. 2003b: Opposite changes in the resistance to cold and desiccation, which occur during the development of the millipede Polydesmus angustus (Diplopoda: Polydesmidae). *Eur. J. Entomol.* **100**: 25–30.

ENGHOFF H., DOHLE W. & BLOWER J.G. 1993: Anamorphosis in millipedes (Diplopoda) – the present state of knowledge with some developmental and phylogenetic considerations. *Zool. J. Linn. Soc.* **109**: 103–234.

FOX C.W. 1993: The influence of maternal age and mating frequency on egg size and offspring performance in Callosobruchus maculatus (Coleoptera: Bruchidae). *Oecologia* **96**: 139–146.

FOX C.W. & CZESAK M.E. 2000: Evolutionary ecology of progeny size in arthropods. *Annu. Rev. Entomol.* **45**: 341–369.

FOX C.W. & MOUSSEAU T.A. 1998: Maternal effects as adaptations for transgenerational phenotypic plasticity in insects. In Mousseau T.A. & Fox C.W. (eds): *Maternal Effects as Adaptations*. Oxford University Press, New York, pp. 159–177.

GIRON D. & CASAS J. 2003: Mothers reduce egg provisioning with age. *Ecol. Lett.* **6**: 273–277.

GONÇALVES S.C., PARDAL M.A., CARDOSO P.G., FERREIRA S.M. & MARQUES J.C. 2005: Biology, population dynamics and secondary production of Tylos europaeus (Isopoda: Tylidae) on the western coast of Portugal. *Mar. Biol.* **147**: 631–641.

GRUNDY A.J. & SUTTON S.L. 1989: Year class splitting in the woodlouse Philoscia muscorum explained through studies of growth and survivorship. *Holarct. Ecol.* **12**: 112–119.

HOPPER K.R. 1999: Risk-spreading and bet-hedging in insect population biology. *Annu. Rev. Entomol.* **44**: 535–560.

KISS B. & SAMU F. 2005: Life history adaptation to changeable agricultural habitats: developmental plasticity leads to cohort-splitting in an agrobiont wolf spider. *Environ. Entomol.* **34**: 619–626.

MASAKI S. 2002: Ecophysiological consequences of variability in diapause intensity. *Eur. J. Entomol.* **99**: 143–154.

MENU F. & DESOUHANT E. 2002: Bet-hedging for variability in life cycle duration: bigger and later-emerging chestnut weevils have increased probability of a prolonged diapause. *Oecologia* **132**: 167–174.

MOHAGHEGH J., DE CLERCQ P. & TIRRY L. 1998: Effects of maternal age and egg weight on developmental time and body weight of offspring of Podisus maculiventris (Heteroptera: Pentatomidae). *Ann. Entomol. Soc. Am.* **91**: 315–322.

MOREIRA G.R.P. & PECKARSKY B.L. 1994: Multiple developmental pathways of Agnetina capitata (Plecoptera: Perlidae) in a temperate forest stream. *J. North Am. Benthol. Soc.* **13**: 19–29.

MOUSSEAU T.A. & DINGLE H. 1991: Maternal effects in insect life histories. *Annu. Rev. Entomol.* **36**: 511–534.

NYLIN S. & GOTTHARD K. 1998: Plasticity in life-history traits. *Annu. Rev. Entomol.* **43**: 63–83.

PRITCHARD G. 1980: Life budgets for a population of Tipula sacra (Diptera: Tipulidae). *Ecol. Entomol.* **5**: 165–173.

QUINN G.P. & KEOUGH M.J. 2002: *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, 537 pp.

ROFF D.A. 2002: *Life History Evolution*. Sinauer, Sunderland, MA, 527 pp.

ROSSITER M.C. 1991: Maternal effects generate variation in life-history: consequences of egg weight plasticity in the gypsy moth. *Funct. Ecol.* **5**: 386–393.

ROSSITER M.C. 1998: The role of environmental variation in parental effects expression. In Mousseau T.A. & Fox C.W. (eds): *Maternal Effects as Adaptations*. Oxford University Press, New York, pp. 112–134.

SEGER J. & BROCKMANN H.J. 1987: What is bet-hedging? In Harvey P.H. & Partridge L. (eds): *Oxford Surveys in Evolutionary Biology. Vol. 4*. Oxford University Press, Oxford, pp. 182–211.

SNIDER R.M. 1984: The ecology of Polydesmus inconstans (Diplopoda: Polydesmidae) in Michigan woodlots. *Pedobiologia* **26**: 185–195.

STEARNS S.C. 1992: *The Evolution of Life Histories*. Oxford University Press, Oxford, 249 pp.

SUNDERLAND K.D., HASSALL M. & SUTTON S.L. 1976: The population dynamics of Philoscia muscorum (Crustacea, Oniscoidea) in a dune grassland ecosystem. *J. Anim. Ecol.* **45**: 487–506.

TAUBER M.J., TAUBER C.A. & MASAKI S. 1986: *Seasonal Adaptations of Insects*. Oxford University Press, New York, 411 pp.

THOMAS J.A., ELMES G.W. & WARDLAW J.C. 1998: Polymorphic growth in larvae of the butterfly Maculinea rebeli, a social parasite of Myrmica ant colonies. *Proc. R. Soc. Lond. (B)* **265**: 1895–1901.

TORCHIO P.F. & TEPEDINO V.J. 1982: Parsivoltinism in three species of Osmia bees. *Psyche* **89**: 221–238.

YANAGI S.I. & MIYATAKE T. 2002: Effects of maternal age on reproductive traits and fitness components of the offspring in the bruchid beetle, Callosobruchus chinensis (Coleoptera: Bruchidae). *Physiol. Entomol.* **27**: 261–266.

ZIMMER M. & KAUTZ G. 1997: Breeding phenological strategies of the common woodlouse Porcellio scaber (Isopoda: Oniscidea). *Eur. J. Soil Biol.* **33**: 67–73.

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